Ecosystems as Functional Units in Nature

John M. Blair, Scott L. Collins and Alan K. Knapp

In the last two decades or so, the word "ecosystem" has become increasingly used by the media and in nonscientific public and private sectors to denote some portion of the natural world, ranging in size and scope from a rotting log to the entire planet on which life as we know it exists. It also has become associated with environmental issues, and with certain land use practices and management approaches (e.g., ecosystem management). This variable and sometimes vague use of the term ecosystem has led to some confusion regarding the meaning of this important ecological concept. Our objectives in this essay are to define the ecosystem concept and briefly describe ecosystem ecology as a scientific discipline. We then provide some examples of ecosystem research and how human activities can impact ecosystems. Finally, we link ecosystem research to the recently conceived concept of ecosystem management and discuss the potential for using knowledge of how ecosystems function to achieve desired management goals.

The ecosystem concept has been used in many contexts. In the scientific realm, the term ecosystem is used most often to describe a relatively discrete unit of nature, such as a lake, a grassland, or a forested mountain valley. Such a view is consistent with much current ecosystem-based research in which the units of study are often well-delineated watersheds, or catchment basins, which are areas defined by topographic features and a common hydrologic drainage. Ecosystem research also includes studies of processes within these entities, such as the flow of energy from plants to consumers (e.g., animals, fungi, bacteria), or the processes determining the amount of soil nitrogen available for use by plants. Research concerned with these processes is a cornerstone of ecosystem science, but such research is not necessarily constrained by a need for ecosystems with distinct physical boundaries. A third use of the ecosystem concept is based on the application of principles derived from ecosystem ecology to achieve certain management goals. An example of this usage would be the Greater Yellowstone Ecosystem that includes Yellowstone and Grand Teton National Parks, surrounding public and private lands, human settlements, and multiple types of other land use. Thus the ecosystem concept can apply to the description and study of a distinct entity, such as a grassland or forested watershed; a process or collection of processes, such as nitrogen cycling; or a management unit like the Greater Yellowstone Ecosystem. Use of the ecosystem concept in all of these contexts is appropriate, when defined explicitly.

Ecosystem ecology as a scientific discipline has relatively recent origins. Although the term ecosystem was coined in 1935 by the British ecologist Arthur Tansley, ecosystem ecology did not begin to flourish as a scientific discipline until the 1960s. Several factors, including an influx of new funding for ecological research, an increase in academic positions at universities, the development of computer technology, and an increased awareness of the effects of human activities on the environment, combined to enhance the development of ecosystem ecology as an important new area of ecological study. Indeed, the influx of new academics after World War II as a result of the GI Bill and growth in American academic institutions, followed by an infusion of research funding for the International Biological Program (IBP) in the 1960s and 1970s, helped build a cadre of ecosystem scientists in the US. One goal of the IBP was to understand patterns and controls of net primary productivity, an ecosystem process, on a global scale. Primary productivity is a measure of the key process of energy capture and energy use by plants on earth. For the first time, teams of ecosystem scientists around the world worked together on a well-funded, common research theme. Computer technology allowed the development of simulation models to predict the consequences of natural and anthropogenic factors on ecosystems. Environmental concerns also influenced the development of ecosystem science. For instance, concerns about the impacts of radiation and during the Cold War era led ecologists in the 1950s and 1960s to study the effects of chronic gamma radiation on ecosystems at the Brookhaven National Laboratory on Long Island. Together, these factors enhanced the growth of ecosystem science in the U.S. and the relevance of this discipline for addressing important environmental issues. Indeed, ecosystem science was one of the first of ecological disciplines to ex-

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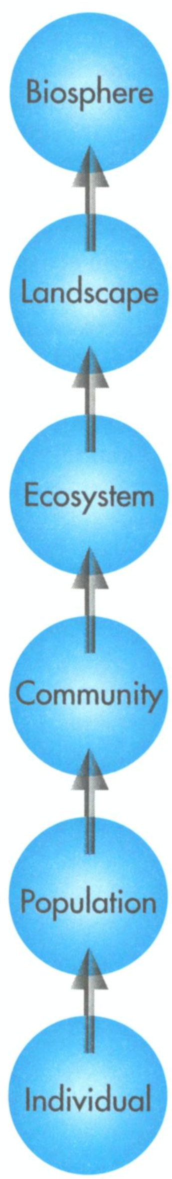
Dr. Blair and Dr. Knapp are professors at Kansas State University and can be reached at jblair@ksu.edu and aknapp@ksu.edu, respectively. Dr. Collins is an adjunct professor at Kansas State University and can be reached at scollins@nsf.gov.

plicitly include the impact of human populations and activities as part of its comprehensive research agenda.

Just What Is an Ecosystem?

An ecosystem can be described in simple terms as a biological community (all of the organisms in a given area) plus its abiotic (nonliving) environment. In fact, the word ecosystem was first used by Tansley to describe natural systems in a way that encompassed all of the living organisms occurring in a given area and the physical environment with which they interact. In this sense, the ecosystem is the first level in the traditional hierarchical arrangement of biological systems (Figure 1). It explicitly includes both living organisms and the abiotic environment as integral parts of a single system. This is one reason that ecosystem studies often focus on quantifying transfer of energy and materials between living organisms and the physical environment.

Figure 1. The traditional hierarchical arrangement of biological systems. The lowest ecological level shown is the *individual*, although that level can also be broken down into subunits (e.g., organs, cells, organelles). A *population* is a group of individuals of the same species that can potentially interact because of spatial proximity. A *community* is a group of interacting populations. Like some ecosystems, many communities are difficult to define spatially. Ecosystems encompass all of the biotic interactions of the levels below, and are the first level in the hierarchy where biotic and abiotic factors interact explicitly through exchanges of energy and matter. *Landscapes* are heterogeneous areas composed of different ecosystems. Finally, the *biosphere* is that portion of earth where life occurs.



Tansley originally described the ecosystem as part of a continuum of physical systems in nature, and in fact the concept of "system" and much of the language used to describe ecosystem structure and function are borrowed from physics. In very general terms, a system is any collection of components, interacting in an organized manner to form a unit, through which may flow materials, energy and information. An ecosystem is a particular kind of system, defined by Eugene P. Odum, a leading proponent of ecosystem ecology, as any unit in nature that includes all the organisms that function together in a given area and their abiotic environment, interacting so that energy flows lead to biotic structure and material cycles. ODUM, BASIC ECOLOGY (1983).

The definition above implies that ecosystems occupy a given area, and that they therefore have boundaries (at least conceptually). Indeed, some ecosystems have fairly obvious, distinct boundaries (a lake, an urban forest, a distinct watershed); but more often the boundaries of an ecosystem are much less distinct and may be user-defined. The concept of the ecosystem as a real physical entity sometimes presents problems, especially in terrestrial habitats, where it is often difficult to say where one ecosystem ends and another begins. Further, boundaries which might be appropriate for quantifying hydrologic fluxes or nutrient budgets may not apply to more mobile or migratory organisms. However, the difficulty in defining precise boundaries does not negate the value of the ecosystem concept, and many ecosystem ecologists simply define their ecosystems based on the area under study. Indeed the same difficulties in defining precise boundaries apply to natural populations and communities; yet these organizational levels are widely accepted and used by ecologists and provide the basis for many management-related decisions.

The "biotic structure" of an ecosystem refers to the community of organisms within the ecosystem, the structure of that community, and the ways in which the organisms comprising it are linked together. The community can be described in terms of trophic structure and biodiversity. Trophic structure refers to feeding relationships and food webs within the community. Biodiversity generally refers to the number of different species and their relative abundance in a given area but also can include genetic diversity within a species and functional diversity within the community.

Ecosystems as functional units include components that interact through the flow of energy and cycling of materials (see Figure 2, page 152). The various components of an ecosystem can be grouped together into three or four major subsystems: the autotrophic subsystem, which is made up of producers such as plants; the heterotrophic subsystem, which is made up of consumers such as animals and microbes. This subsystem can be further subdivided into grazing and decomposer (detrital) foodwebs, based on where the link with the producer subsystem occurs. Abiotic materials, such as the mineral soil, stored organic matter, water, and mineral nutrients, are part of the abiotic subsystem.

A Process-Based View of Ecosystems

An alternate way of viewing an ecosystem is based on the processes that comprise ecosystem functioning. These processes include productivity, energy flow among trophic levels, decomposition, and nutrient cycling. In this way, an ecosystem can be defined based on the collection of processes required to continue normal functioning, as opposed to the physical boundaries within which those processes operate. Defining what constitutes "normal" functioning is a critical issue, with important implications for preserving and managing ecosystems. Some early proponents of the ecosystem concept viewed ecosystems as highly integrated collections of organisms which would achieve a stable equilibrium (the "balance of nature") in the absence of outside disturbances. However, this view has largely been replaced by a non-equilibrium perspective in which disturbances are seen as natural phenomena. Thus, defining a natural disturbance regime and the boundaries of ecosystem functioning are challenges for both ecosystem scientists and ecosystem managers.

Ecosystems function by processing energy and materials, operating under certain internal constraints or rules and producing certain outputs. Systems, by definition, have boundaries that delimit them from their surroundings, or their environment. An important aspect of ecosystems, however, is that they are "open" systems with respect to both materials and energy. They are subject to an input environment (beyond the system boundaries), which includes inputs of energy (e.g., sunlight) and materials (e.g., water and nutrients). These inputs can cause changes in the internal components of an ecosystem (compartments called state variables) over time. The interactions of inputs and state variables affect ecosystem processes and result in ecosystem outputs, or an output environment. For example, inputs of water and carbon dioxide in combination with state variables such as soil nutrients and plants leads to primary productivity—an ecosystem process—that may be consumed by grazers and transported to another ecosystem. Inputs that play a major role in altering ecosystem components and outputs are also referred to as forcing functions. For example, sunlight, water and nutrients are important forcing functions that affect the structure and functioning of most ecosystems. Natural disturbances, such as periodic fires or hurricanes, also play a role in affecting ecosystem structure and function. It is also important to note that the open nature of ecosystems means that the output environment of one ecosystem becomes part of the input environment of another. Thus, flows of material and energy link ecosystems in the biosphere.

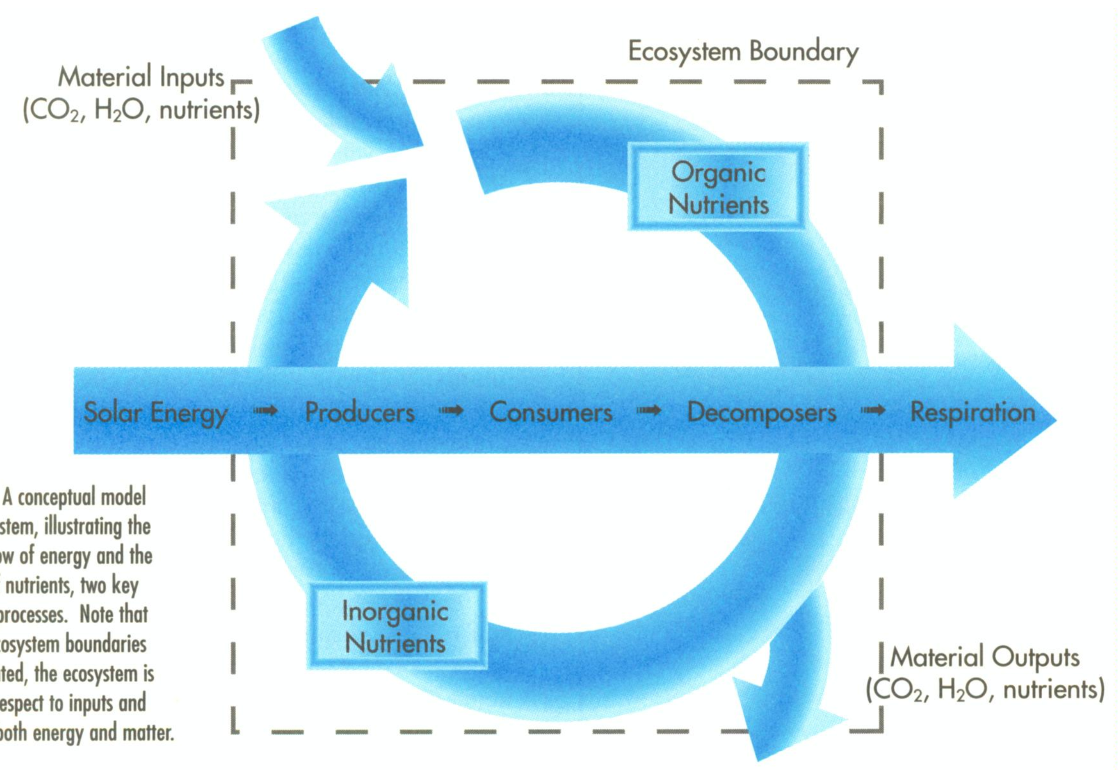


Figure 2. A conceptual model of an ecosystem, illustrating the one-way flow of energy and the recycling of nutrients, two key ecosystem processes. Note that although ecosystem boundaries are designated, the ecosystem is open with respect to inputs and outputs of both energy and matter.

Although ecosystems are open with respect to flows of both energy and materials, the behaviors of energy and materials, once they are in ecosystems, fundamentally differ. Energy transformations are essentially one-way flows, and thus energy cannot be recycled or reused within an ecosystem. Nutrients, however, can circulate or cycle within an ecosystem, and the flow of nutrients among different compartments is referred to as nutrient cycling. Nutrients include substances such as phosphorus, nitrogen, potassium, and calcium that are required by living organisms. Because the flows of chemical nutrients typically involve both biological (organic) and geological (inorganic) pools, nutrient cycles also are referred to as biogeochemical cycles. Ecosystem ecologists are often interested in describing and quantifying the storage and movement of nutrients among these pools, as well as understanding the factors that regulate these patterns of movement. This is important from both theoretical and practical perspectives. Unwanted, and unintended, changes in nutrient cycles can have profound consequences for environmental quality and human populations (e.g., groundwater contamination, acid rain, global climate change, eutrophication of lakes).

Virtually all ecosystems depend on a continual input and output of energy to maintain their internal structure and function, and therefore are classified as thermodynamically open systems. Ecosystems can be thought of as energy-transforming machines that must conform to the first and second laws of thermodynamics. Energy enters an ecosystem, is processed and transformed to do work, and is eventually dissipated as heat through the metabolic respiration of living organisms. In most ecosystems, inputs of solar energy act as the "fuel" for photosynthesis, and the feeding relationships and efficiencies of energy flow among trophic levels (links in a food chain, such as herbivore, primary predator, secondary predator, etc.) establish the rates of energy flux. There are, however, ecosystems that are dependent on natural subsidies of energy from other ecosystems (e.g., a small woodland stream receives most of its energy in the form of dead leaves from the surrounding forest), and many human-dominated ecosystems depend on fossil-fuel subsidies to run machinery and to manufacture fertilizers and pesticides.

Nutrients, on the other hand, can be recycled within ecosystems and reused many times. In fact, one way of delineating ecosystem boundaries is through nutrient cycles. Most ecosystems recycle more nutrients annually than they receive as "new" inputs. Although nutrients do cycle within ecosystems, they are continually being lost, often in small quantities, and must be replaced with new inputs. In natural ecosystems, these new inputs come in the form of nutrients added in precipitation by weathering of rock and soil, or, in the case of nitrogen, through biological fixation of atmospheric nitrogen. Many human activities can alter, either directly or indirectly, the efficiency with which nutrients are recycled and retained in ecosystems. These changes often have negative consequences for ecosystems "downstream" (e.g., reduced water quality as nutrients and sediments are released from disturbed ecosystems). In a similar way, changes in nutrient inputs can have a variety of negative impacts in many ecosystems.

The Ecosystem as an Entity: The Hubbard Brook Ecosystem Study

A good example of the structure and associated function in a clearly bounded ecosystem comes from the well-studied Hubbard Brook Experimental Forest in the White Mountains of New Hampshire. Hubbard Brook is the main outflow stream in this experimental forest. It is fed by smaller streams that drain clearly defined watersheds in these mountains. Because of the topography and the underlying granite bedrock, there are distinct and discrete pathways for the movement of water and nutrients into and out of these small watersheds. The U.S. Forest Service has been monitoring the flow rates and water chemistry (pH, nitrogen, phosphorus, turbidity) of these streams since the early 1960s. Ecologists with the Forest Service and several universities were interested in determining the role of the vegetation in controlling nutrient cycling and outputs and ecosystem responses to clear-cutting in this region. A whole-ecosystem research program was initiated by comparing nutrient fluxes on a watershed that was clear-cut in 1966 to an adjacent control watershed that was not cut.

Following clear-cutting, water chemistry changed dramatically in the stream draining the clear-cut watershed. Amounts of nitrogen and cation nutrients, such as potassium and calcium, increased in the stream water, and the water became more turbid. As vegetation regrowth occurred following clear-cutting, nutrient levels in stream water decreased dramatically. This study clearly demonstrated the important role of the biota, particularly plants, in the retention and recycling of nutrients in ecosystems. This long-term research project continues today, with the goal of documenting long-term patterns of forest ecosystem recovery following disturbance. One of the unexpected consequences of long-term research at the Hubbard Brook site was the discovery of the impact of acid rain on ecosystems in the northeastern United States. Because of the long-term record of stream chemistry and measurement of atmospheric inputs in these watersheds, ecosystem research at Hubbard Brook produced solid documentation of the detrimental effects of acid rain on ecosystem function, and helped to justify passage of the acid rain portions of the Clean Air Act Amendments of 1990. In addition, this long-term research program has documented the positive impact of that legislation as acid rain has declined over time.

Ecosystem Processes and the Role of Fire in Tallgrass Prairie

Konza Prairie, a long-term ecological research site in northeastern Kansas, provides an example of the importance of disturbances, and how ecosystem structure and function can be studied at spatial scales that do not necessarily coincide with distinct ecosystem boundaries. Konza Prairie is part of a large expanse of tallgrass prairie that extends from northeastern Kansas southward into northeastern Oklahoma. Fire is an integral part of these tallgrass prairie ecosystems, altering many aspects of prairie ecosystem structure and functioning. The high productivity of tallgrass prairie provides large accumulations of fine, combustible fuel in the form of dead grass, and fires were thought to have been widespread and common in the history of these grasslands. Fire also plays an essential part in the management of present-day tallgrass prairies, where it is used to limit the growth of woody plants and to promote the growth and vigor of the dominant warm-season grasses such as big bluestem. These grasses are the primary food source of domestic cattle in the tallgrass region of the United States. Due to its importance in the development and persistence of tallgrass prairie, studies of the effects of fire on ecosystem processes have been a major emphasis of research at Konza Prairie.

More than twenty years of research at Konza has shown that spring burning generally increases total plant productivity by stimulating growth of the warm-season grasses. This results from the removal of dead and decaying plant material (detritus) that accumulates in the absence of fire. This detritus acts as a mulch layer, insulating the soil surface and limiting light availability for plants early in the growing season. The removal of surface detritus and standing dead plants by fires in early April result in warmer soils and greater light availability for emerging plants. These changes in the soil microclimate promote the growth of the dominant warm season grasses. The increased growth of the grasses also increases their ability to compete with other plant species, leading to another effect of frequent fires—a reduction in the abundance and diversity of many cool-season plants, including the wildflowers that provide much of the biodiversity in tallgrass prairie. Thus, frequent burning increases productivity of forage grasses but lowers plant diversity, at least in ungrazed prairie.

Fire also alters other ecosystem processes, including nutrient cycling. The most important effects involve changes in the cycling of nitrogen, an important consideration for the management of tallgrass ecosystem and for sustainable use of these grasslands for cattle production. Nitrogen is an essential plant nutrient that often is in short supply relative to plant demand, and the availability of nitrogen limits the growth of both plants and animals in many ecosystems. Research at Konza Prairie, however, has shown that nitrogen limitation to plants in tallgrass prairie varies with different management practices. When a prairie burns, most of the nitrogen contained in surface detritus and plants is converted to gaseous forms and lost to the atmosphere. Thus, frequent fires may lead to a substantial loss of the prairie's nitrogen capital in ungrazed prairie. Grazing by cattle, however, may help to conserve nitrogen in burned prairie ecosystems by reducing the amount of detritus and, thus, limiting the amount of nitrogen lost in a fire. N. Thompson Hobbs et al., *Fire and Grazing in the Tallgrass Prairie: Contingent Effects on Nitrogen Budgets*, 72 ECOLOGY 1374 (1991). This example demonstrates the importance of process-level ecosystem studies for understanding and predicting grassland ecosystem responses to burning and grazing as both natural disturbances and management practices.

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Ecosystem management. Ecosystem management has been defined as "management driven by explicit goals, executed by policies, protocols, and practices, and made adaptable by monitoring and research based on our best understanding of the ecological interactions and processes necessary to sustain ecosystem composition, structure, and function." Norman L. Christensen et al., *The Report of the Ecological Society of America Committee on the Scientific Basis for Ecosystem Management*, 6 ECOLOGICAL APPLICATIONS 665 (1996). This definition includes both common uses of the term ecosystem discussed earlier—the ecosystem as a functional and identifiable unit in nature—and ecosystem processes (such as nitrogen cycling). In this case the goal is to manage a defined ecosystem, often to provide a product (e.g., water, wood products, beef) while sustaining natural processes that include ecosystem services, such as purification of air and water, regeneration of soil nutrients, and maintenance of biodiversity. As noted by Costanza, d'Arge and de Groot in *The Value of the World's Ecosystem Services,* 387 NATURE 253–260 (1997), the monetary value of these services is tremendous. As our understanding of the processes occurring within and among ecosystem components increases, ecosystem management may provide a viable strategy for sustainable use of natural resources. For this to be realized, knowledge of the inputs, processes and cycles, and outputs of a managed ecosystem is required. This may be most feasible in clearly defined ecosystems, such as the watersheds at Hubbard Brook, where the natural boundaries are relatively well defined and encompass most of the major components necessary for ecosystem functioning. Ecosystem management of less well delineated or more fragmented ecosystems (e.g., a forest fragment surrounded by agricultural fields) will be far more challenging because of the increased interactions with surrounding ecosystems and the potential for greater movement of materials and organisms from the surrounding landscape into and out of the ecosystem of interest.

Such challenges should not be viewed as impediments to ecosystem management, however. The benefits of ecosystem versus species-level management are numerous. Attempts to manage species as entities isolated from their biotic and abiotic environment (the ecosystem) are doomed to failure and the costs associated with the loss of ecosystem services due to mismanagement can be astounding. Clearly, the open nature of ecosystems and their lack of discrete boundaries should not be used as excuses for failing to design policies to manage them. Our legal system is replete with regulations that cross boundaries (e.g., interstate laws) and regulate processes and phenomena that are not discrete entities (e.g., air quality).

Ecosystem management can certainly benefit from the scientific approaches and tools developed as a part of ecosystem ecology. For example, the long-term study of ecosystem structure and processes provides important information on the natural variations that ecologists now recognize occur in all ecosystems. Such information can serve as the basis for detecting disruptions in ecosystem function. Additionally, one of the most important tools for generalizing about the rules governing ecosystem structure and function, and applying this knowledge to the management of ecosystems, is mathematical ecosystem modeling. The development of computer technology and adoption of techniques from physics and electrical engineering has allowed ecologists to create computer simulation models of ecosystems. In early models, an ecosystem was simplified into compartments, or boxes, which were connected by arrows representing the movement of matter and energy. The models focused primarily on the arrows (movement of matter and energy), and the controls on these flows. Because of this representation, an ecosystem was caricatured as a discrete entity, with relatively clear boundaries and discrete functional parts.

Recently, interest has shifted to a greater emphasis on processes (such as nitrogen cycling) within the boxes, and now more detailed process-based ecosystem models have been developed for a variety of applications. That is, computer models such as the Century simulation model, can be used to predict the availability and flow of nutrients in an ecosystem under different hypothetical scenarios (e.g., a surplus of nitrogen or increasing atmospheric carbon dioxide). For example, Timothy R. Seastedt, used the Century model to make predictions about the effects of long-term, frequent burning and grazing on nitrogen cycling, plant productivity, and soil carbon storage in tallgrass prairies. Timothy R. Seastedt et al., *Controls of Plant and Soil Carbon in a Semihumid Temperate Grassland,* 4 ECOLOGICAL APPLICATIONS 344-353. (1994). Thus, model output in combination with empirical studies can be used to assess sustainability issues in ecosystems where cattle production is an important regional commodity. Some predictions of the model, such as increased nitrogen limitation with frequent burning in the absence of grazing, are consistent with data from long-term field studies and have provided important insights into the mechanisms underlying the responses of prairies to fire. Other predictions, such as lower plant productivity and losses of soil organic carbon, have not been supported by long-term measurements, pointing to the need for both modeling and experimentation as important and complementary approaches for ecosystem ecologists.

The ecosystem concept is often applied to well-defined and relatively small geographic entities in nature, where the input and outflow of energy and materials is reasonably well delineated. The main goal of ecosystem ecology as a research discipline is to understand, in detail, the processes of energy capture and the conversion of matter (e.g., nitrogen, carbon) and energy (e.g., sunlight) from one state to another within ecosystems, and the rules that govern these processes. The ecosystem concept, however, can also be applied to systems in nature that are less clearly bounded, including larger geographic areas that often contain several smaller ecosystems in whole or in part. These ecosystems may be more difficult to manage, unless management is scaled to definable subunits. This explains, perhaps, why ecosystem management is better developed in some ecosystems (forested watersheds) than others (coastal ocean areas, large rivers). In fact, it may be more difficult to apply ecosystem management approaches to large ecosystems that interact in many complex ways with the surrounding landscape, as is the case with coastal estuaries. Perhaps that is why many of the most difficult and unpredictable environmental problems (e.g., outbreaks of the toxic marine dinoflagellate *Pfeisteria*) occur in such complex, open systems. The challenges associated with ecosystem management highlight the importance of basic research in ecosystem ecology for understanding how ecosystems work at many different spatial scales. Ecosystem components represent the basic building blocks of complex food webs, of which humans are a part, and ecosystem processes provide many services upon which humans rely. As the impacts of human activities on ecosystem structure and function increase through time, a better understanding of the workings of both natural and managed ecosystems can be combined with predictive models to help manage ecosystems in a sustainable way.